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ESTIMATED FREQUENCIES OF THE BUFF AND GRAY GENES (G, g) IN ADJACENT POPULATIONS OF DEER-MICE (*PEROMYSCUS MANICULATUS BLANDUS*) LIVING ON SOILS OF DIFFERENT COLORS

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INTRODUCTION

THIS report deals with the frequencies of two Mendelian genes which have major effects on pelage color. Gene ratios are estimated for five closely adjacent populations of deer-mice (*Peromyscus maniculatus blandus*) in the Tularosa Basin, New Mexico. The estimated gene frequencies at the five localities are discussed in relation to the color of the soils inhabited by the mice and to the ecological distribution and population dynamics of the species of this area.

Areas of buff and of gray soils occur adjacent to one another in many parts of the Tularosa Basin. Some of the ecological associations on these soil types include considerable populations of deer-mice, and the dynamics and ecological limits of these populations are probably as well known as those of any populations of small mammals. The two genes studied produce a buff and a gray mouse, respectively. The comparative frequencies of these genes for buff and gray pelage on adjacent areas of buff and gray soils should, therefore, afford some measure of the intensity of selection against the mice that are conspicuous on their backgrounds.

ACKNOWLEDGMENTS

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The method for statistical treatment of the data was devised by Charles W. Cotterman, and acknowledgment is gratefully made for his important contribution to the study.

METHODS

Stocks of deer-mice were collected at five localities in the eastern Tularosa Basin from October to December, 1938. The field-caught mice were shipped alive to the Laboratory of Vertebrate Biology at Ann Arbor, Michigan. In the laboratory the buff mice, dominant over gray (Dice, 1933), were mated to gray to determine their genotypes. The offspring of the test cross were classified into color types and then, at an age of approximately five months, prepared as flat skins. The classification was rechecked in the prepared specimens.

LOCALITIES OF ORIGIN OF THE SAMPLES

Samples of the wild populations of deer-mice were obtained at the following localities in the Tularosa Basin:

Tularosa. A total of 108 deer-mice were obtained about three miles north of the town of Tularosa. Deer-mice were concentrated in grassy washes along the right-of-way of the Southern Pacific Railroad and along a few grassy washes and irrigation ditches lateral to the railroad. The soil at this station is dark red.

Alamogordo. This sample of 179 deer-mice was taken about three miles south of the town of Alamogordo. The deer-mice were trapped in an extensive area of mesquite association, where they were numerous. The soil is pinkish gray.

Salinas. Sixty-five deer-mice were trapped along the Southern Pacific right-of-way, seven to twelve miles north of Tularosa. Here, as at Tularosa, the deer-mice were concentrated along the railroad, but the mice were scarcer than they were at the Tularosa station. The soil at this station is pinkish gray.

Lone Butte. A total of fifty-seven deer-mice was obtained in an isolated area of mesquite association covering a few acres about thirteen miles west of the town of Tularosa. The soil is pale pinkish gray.

White Sands. This station is in the interior of the gypsum dunes of the White Sands National Monument. It is in section 19, township 17s, range

7e. The soil is creamy-white gypsum "sand." Deer-mice were scarce here, and only thirteen live mice were secured.

ESTIMATE OF GENE FREQUENCIES

As the basis for estimates of the frequencies of the buff and gray genes in adjacent populations of deer-mice, fairly adequate samples from four wild populations and a small and relatively inadequate sample from a fifth population were secured. The gray, or homozygous recessive, mice were determined by inspection. The dominant buff mice then were mated to gray in order to determine whether or not they were heterozygous for gray. Some dominants had no offspring in the laboratory, and a few that did breed produced less than ten offspring. Some of the dominants were mated *inter se* for another study, and in some instances produced litters containing gray offspring, but they later failed to breed when mated to gray mice. The mice of each stock are grouped into three classes for the estimate of gene frequencies. There are (1) the dominants that produced ten or more offspring in crosses to gray, (2) the dominants that produced less than ten offspring when crossed to gray, and (3) the recessive grays, which were determined by inspection.

In estimating the population gene ratio from such data, an approximation may be introduced without appreciable bias or serious loss of precision. I shall ignore the offspring of all buff mice, each of which did not produce ten or more offspring in test crosses with gray, even though some are known heterozygotes. By classifying all such dominants as "untested," a small amount of information is sacrificed, although no bias will be introduced if the progenies are discounted regardless of their composition. Now, the chance that a heterozygous buff mouse should produce ten or more offspring, all buff, is only 1/1024 or less. By classifying such dominants as homozygous, the estimate of gene frequency should be biased in favor of the dominant gene by a small and negligible amount.

Each original sample of wild-caught mice may therefore be classified in four categories: (1) buff, untested, (2) buff, homozygous, (3) buff, heterozygous, and (4) gray. The observed frequencies in these four classes will be designated a, b, c, and d, respectively, their total being n. If all dominants had been tested ($a = 0$), the frequency of the recessive gene, would be estimated as

$$q = \frac{c + 2d}{2n}, \text{ with standard error, } s = \frac{\sqrt{q(1-q)}}{2n},$$

whereas if all dominants were untested ($b = 0$, $c = 0$), one could take as the estimate, assuming genetic equilibrium,

$$q = \sqrt{\frac{d}{n}}, \text{ with standard error, } s = \frac{\sqrt{1-q^2}}{4n}$$

(Cotterman, 1946). When dominants are only partly classified as to genotype, as in the present instance, a weighted estimate having an intermediate precision is required.

If k represents the proportion of dominants tested, $(b+c)/(a+b+c)$, the expected frequencies (m) in the four classes are as shown in Table I.

TABLE I

Expected Frequencies of Classes of Genotypes When Part of the Dominants are Untested

Class	Observed Frequency X	Expected Frequency m
Dominants, untested	a	$(1-q^2)(1-k)n$
Dominants, homozygous	b	$(1-q)^2kn$
Dominants, heterozygous	c	$2q(1-q)kn$
Recessives	d	q^2n
Total	n	n

Applying the method of maximum likelihood (Fisher, 1945) to this table, one obtains the estimate

$$q = \frac{\sqrt{(2b+c)^2 + 8n(c+2d)} - (2b+c)}{4n}, \qquad (1)$$

and its standard error is given by

$$s = \sqrt{\frac{q(1-q^2)}{2n(k-kq+2q)}}. \qquad (2)$$

When $k=0$ or $k=1$, these formulae reduce to those given above for the cases of genes with or without dominance, respectively.

If (1) and (2) are applied to the data on buff and gray at each collecting station the estimated frequency (q) of recessive gray genes is found for each of the five populations (Table III). Using these estimates one may calculate the expected frequencies from Table I and test the goodness of fit of the data to the single-gene hypothesis and the assumption of genetic equilibrium (Table II).

Actually, only the assumption of genetic equilibrium is tested here. It is already known that the major differences between the buff and gray mice represent the effects of a single gene (Dice, 1933; Blair, 1947). Therefore, any significant deviations from the expected frequencies may be taken as indications of a departure from genetic equilibrium. Only one degree of freedom remains for the chi-square test since, although there are four classes, the expectations have been made to agree with the observations in respect to n, p, and k. Applying this test, one finds no significant deviations from the expected frequencies in the four major samples (Table II). All of the χ^2 values fall below 3.841, which marks the 5 per cent level of probability. In the White Sands sample, which is too small for a reliable test of significance, the observed numbers fall fairly close to the expected. It is evident, then, that at least four of the populations sampled are within sample bounds as regards the distribution of genotypes. The character of the fifth, small sample suggests that the population from which it was drawn is also in equilibrium.

COMPARATIVE GENE FREQUENCIES IN THE TULAROSA BASIN POPULATIONS

As an estimate of the frequencies of the buff and gray genes in deer-mice populations of five localities in the Tularosa Basin (Table III) has been obtained, these estimates can be compared to ascertain whether or not the two genes are equally distributed in the total deer-mouse population of the basin (Table IV).

TABLE II

Observed and Expected Frequencies of Buff and Gray Genotypes in Samples of Deer-mice from Five Stations in the Tularosa Basin, New Mexico

Sample and Class	Observed Frequency X	Expected Frequency m	$(X-m)^2/m$ χ^2
Tularosa			
Buff, untested	52	51.88	0.0003
Buff, homozygous	14	14.23	0.0037
Buff, heterozygous	22	21.69	0.0044
Gray	20	20.19	0.0018
Total	108	107.99	0.0102
Alamogordo			
Buff, untested	32	31.06	0.0285
Buff, homozygous	4	6.48	0.9491
Buff, heterozygous	43	39.13	0.3828
Gray	97	99.34	0.0551
Total	176	176.01	1.4155
Salinas			
Buff, untested	37	36.68	0.0028
Buff, homozygous	5	5.57	0.0583
Buff, heterozygous	10	9.30	0.0527
Gray	13	13.45	0.0151
Total	65	65.00	0.1289
Lone Butte			
Buff, untested	7	6.61	0.0230
Buff, homozygous	4	6.10	0.7230
Buff, heterozygous	25	21.28	0.6503
Gray	21	23.01	0.1756
Total	57	57.00	1.5719
White Sands			
Buff, untested	2	1.84	
Buff, homozygous	0	0.50	
Buff, heterozygous	4	3.17	
Gray	7	7.48	
Total	13	12.99	

The Tularosa and Salinas samples do not differ significantly in their estimated frequencies of buff and gray genes, and it is inferred that they were drawn from populations having the same parameters in respect to this frequency. Likewise, there is no significant difference in the buff–gray ratio among the Alamogordo, Lone Butte, and White Sands mice. In all other comparisons between any two of the populations the differences in gene ratio

TABLE III

ESTIMATED FREQUENCIES OF THE BUFF (G) AND GRAY (g) GENES IN POPULATIONS OF DEER-MICE (*Peromyscus maniculatus blandus*) AT FIVE STATIONS IN THE TULAROSA BASIN, NEW MEXICO, IN PER CENT WITH STANDARD ERRORS

Station	Soil Color	Estimated Frequencies		Standard Errors
		Buff (G)	Gray (g)	
Tularosa	Dark Red	56.76	43.24	3.85
Alamogordo	Pinkish gray	24.87	75.13	2.37
Salinas	Pinkish gray	54.51	45.49	5.10
Lone Butte	Pale Pinkish gray	36.46	63.54	4.61
White Sands	Creamy white	24.13	75.87	8.59

are significant beyond the 1 per cent level of probability. The Alamogordo, Lone Butte, and White Sands mice all have a significantly higher proportion of gray genes than do those from Tularosa and Salinas. The Alamogordo mice have a somewhat, but not significantly, higher proportion of gray genes than do those of the Lone Butte station.

OTHER COLOR VARIATION

The shade of pelage color in the four major samples of deer-mice has been measured by a photovolt reflection meter using a standard technique (Blair, 1947). The reflection meter values are expressed as the percentages of light reflected from designated areas of the dry mouse skin by comparison with the light reflected from a magnesium block. Three color filters, red, green, and blue, have been used.

The buff mice from Tularosa and Salinas do not differ significantly ($t = 2.6$ or more) in any of the color readings (Table IV). Both the Tularosa and Salinas buffs, however, average significantly lower (i.e., darker in shade of pelage) than do the Alamogordo and Lone Butte buffs in all reflection meter readings except dorsal blue. The Tularosa mice to not differ

TABLE IV

COMPARISON OF BUFF (G): GRAY (g) RATIOS IN FIVE DEER-MOUSE POPULATIONS OF THE TULAROSA BASIN, NEW MEXICO

Comparisons	Gene Ratio Differences in Per Cent	t
Tularosa—Salinas	2.25 ± 6.39	0.35
Tularosa—Alamogordo	31.89 ± 4.52	7.06
Tularosa—Lone Butte	20.30 ± 6.01	3.38
Alamogordo—Lone Butte	11.59 ± 5.19	2.23
Salinas—Lone Butte	18.05 ± 6.88	2.62
Salinas—Alamogordo	29.64 ± 5.62	5.27
White Sands—Tularosa	32.63 ± 9.41	3.47
White Sands—Salinas	30.38 ± 9.99	3.04
White Sands—Alamogordo	0.74 ± 8.91	0.08
White Sands—Lone Butte	12.33 ± 9.75	1.26

significantly from either the Alamogordo or the Lone Butte buffs in reflected mid-dorsal blue. The only significant difference between the Alamogordo and Lone Butte buffs is in the value for reflected green; Lone Butte is higher than Alamogordo.

The gray mice from Lone Butte are slightly but significantly higher in readings for mid-dorsal green than are those from Alamogordo. The other gray mice of the four stocks do not differ significantly in any of the color readings. This apparent uniformity of the grays, however, can be given little weight, for the numbers are small in three of the stocks, and the standard errors consequently are large.

From these data, one may deduce that the Tularosa and Salinas samples are drawn from populations having the same parameters for minor, additive genes affecting the saturation and intensity of pigment in the major phenotypes (Blair, 1947). The Alamogordo and Lone Butte samples come from other populations having approximately common parameters in respect to these minor genes.

DISTRIBUTION OF DEER-MOUSE POPULATIONS IN THE TULAROSA BASIN

Deer-mice are widely, but not evenly, distributed in the Tularosa Basin. The deer-mice are limited largely to the mesquite and grassy wash associations, and they occur only rarely in the creosote-bush and atriplex associations (Blair, 1943*a*). Because of strong edaphic controls these ecological associations are discontinuously distributed in the basin. Local areas of mesquite or grassy wash association are separated by extensive areas of creosote bush and atriplex that undoubtedly act as partial barriers to the dispersal of deer-mice. A limited amount of dispersal of deer-mice probably takes place through these unfavorable associations, but it must be of much less magnitude than the dispersal within the limits of a widely distributed favorable ecological community.

The Tularosa, Salinas, and Alamogordo samples constitute a north-south transect through the eastern edge of the basin, parallel to and about three miles distant from the foothills of the Sacramento Mountains. At Tularosa and Salinas the deer-mice were living in grassy washes along a railroad and on the grassy and weedy banks of a few irrigation ditches lateral to the railroad. Creosote-bush association, which is unfavorable to deer-mice, occupies the alluvial slopes adjacent to the foothills and extends into the basin beyond the railroad and is replaced by atriplex association toward the interior. The grassy-wash association inhabited by the mice occupies the floor and sides of a dry drainage ditch paralleling the railroad, and nowhere is the association more than a few yards wide. Extensive trapping in the creosote-bush association resulted in the capture of only two deer-mice. The creosote-bush association is, therefore, at least a partial barrier to the dispersal of deer-mice, and the population along the railroad probably approaches linearity. This condition, of course, has existed only since the

TABLE V

MINOR COLOR VARIATIONS IN FOUR SAMPLES OF DEER-MICE FROM THE TULAROSA BASIN, NEW MEXICO
Means and Standard Errors of Reflection-meter Readings

Samples and Phenotypes	No.	Mid-Dorsal			Side		
		Red	Green	Blue	Red	Green	Blue
BUFF							
Tularosa	82	16.12 ± 0.27	9.11 ± 0.17	6.61 ± 0.14	28.61 ± 0.41	16.44 ± 0.30	10.78 ± 0.22
Alamogordo	74	19.16 ± 0.27	9.99 ± 0.18	7.36 ± 0.15	31.23 ± 0.36	18.78 ± 0.28	12.70 ± 0.24
Salinas	42	16.14 ± 0.42	9.02 ± 0.27	6.45 ± 0.18	27.95 ± 0.63	16.29 ± 0.37	10.98 ± 0.33
Lone Butte	33	18.45 ± 0.31	11.03 ± 0.23	7.09 ± 0.17	32.06 ± 0.58	19.12 ± 0.43	12.61 ± 0.36
GRAY							
Tularosa	17	16.47 ± 0.54	10.47 ± 0.35	8.41 ± 0.24	29.29 ± 0.77	19.24 ± 0.58	14.65 ± 0.33
Alamogordo	87	17.72 ± 0.23	10.13 ± 0.15	8.80 ± 0.12	30.20 ± 0.36	19.91 ± 0.26	15.59 ± 0.22
Salinas	10	15.60 ± 0.81	10.50 ± 0.46	8.30 ± 0.40	27.90 ± 1.06	19.00 ± 0.96	14.30 ± 0.47
Lone Butte	20	17.60 ± 0.48	11.20 ± 0.38	8.85 ± 0.33	30.15 ± 0.92	21.45 ± 0.62	16.15 ± 0.54

building of the railroad. Before that time, and before irrigation was begun, any deer-mouse population of this section presumably inhabited the grassy washes draining across the creosote-bush association from the foothills of the mountains.

At Alamogordo the mice live mostly in mesquite association. The sample was obtained near the railroad, but the mice were not restricted to the railroad right-of-way as they were at the other stations. The deer-mice were widely and rather evenly distributed over an area of mesquite association that extends several square miles south of the town of Alamogordo. The Salinas station extends along five miles of the railroad from a point four miles north of the Tularosa station to a point nine miles north of that station. The Alamogordo station is eighteen miles south of the Tularosa station. The grassy washes along the railroad provide a possible route of dispersal of deer-mice connecting all of these stations. The unfavorable creosote-bush association flanking the railroad and occupying most of the territory between the stations probably retards dispersal and largely limits it to a linear type by way of the grassy washes along the railroad.

The Lone Butte and White Sands populations are at least partly isolated from the above-mentioned populations of the eastern basin. The interior of the basin exclusive of the White Sands is largely occupied by atriplex association, which is unfavorable for deer-mice. The Lone Butte mice occupied an area of mesquite association that extends only a few acres. It is separated from the Tularosa population, the nearest of the eastern basin populations, by approximately thirteen miles of atriplex and creosote-bush associations. The sparse population of the White Sands, an area of 270 square miles of gypsum dunes near the middle of the basin, is separated from all of the other populations by atriplex and creosote bush.

DISCUSSION

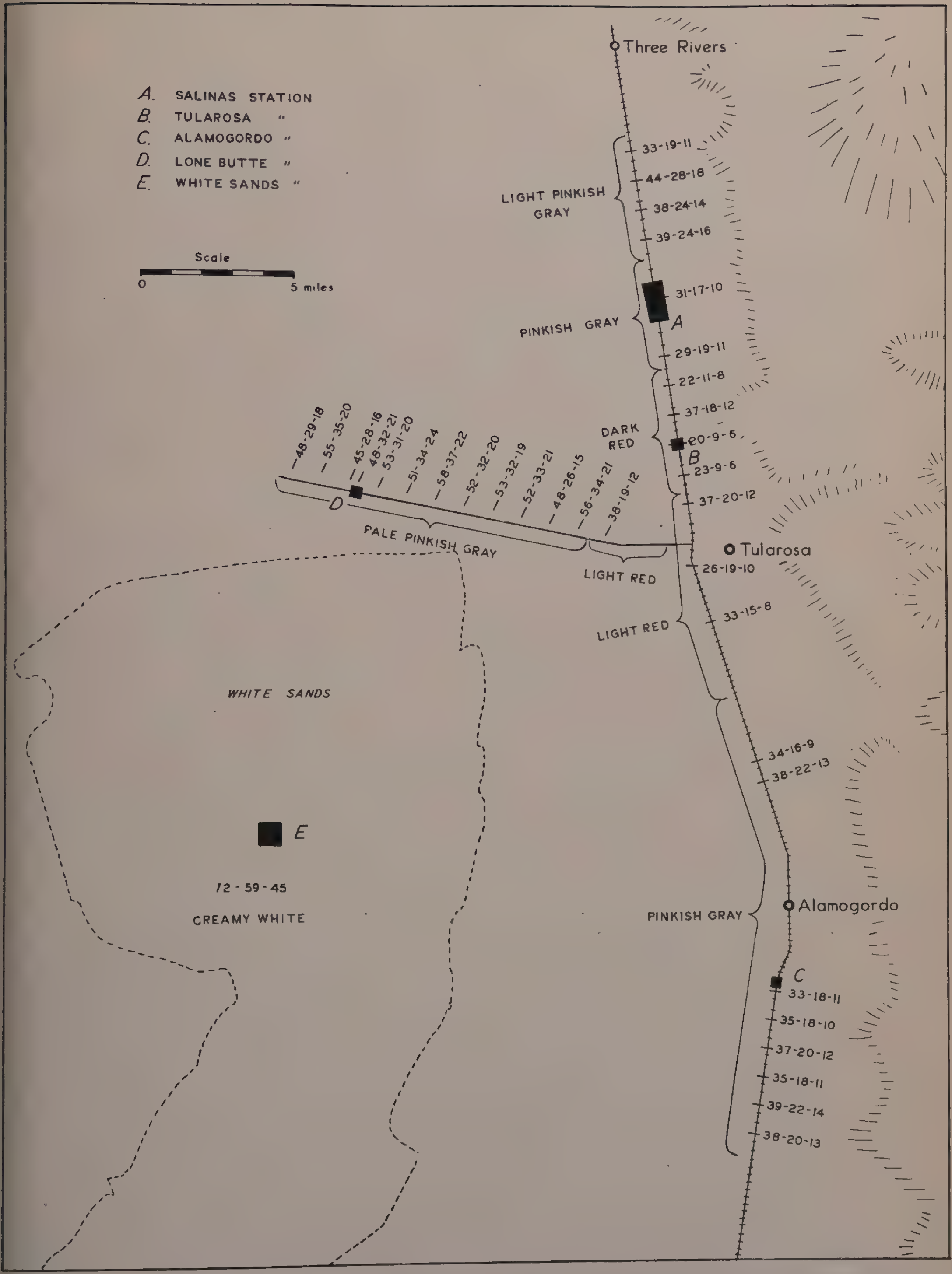
The frequencies of the buff and gray genes in five local populations of deer-mice in the Tularosa Basin have been estimated. I have tested the hypothesis that these genes are in equilibrium in the populations sampled and find that the data support this hypothesis. I have found, further, that the differences between some of the gene ratios exceed the differences that might be expected from sampling variations. Differences in the shade and saturation of the buff phenotype that are attributable to the effects of minor, additive genes have also been found. I have considered the distribution of the deer-mouse population of the Tularosa Basin as it has been determined from ecological studies in the region. An explanation must be sought for the differences and likenesses in buff–gray ratios and for the other genetic color differences within the relatively small area from which the samples were taken.

The genetic differences in the populations sampled might be accounted for in any or all of three ways: (1) isolation by distance and ecological barriers, and consequent random divergence, (2) differential selection pressures at the different localities, and (3) differential mutation rates.

First, there is possibility of random differentiation. Differences in the frequencies of certain gene arrangements in the third chromosome in isolated populations of *Drosophila pseudoobscura* have been attributed to just such random divergence (Dobzhansky and Queal, 1938). The distribution of the deer-mouse population of the Tularosa Basin approximates the "island model" population postulated by Wright (1943) in his mathematical treatment of the effects on gene frequencies of isolation by distance. The local populations are small and at least partly isolated one from the other by ecological barriers. The one probable route of effective dispersal between any of the populations results from recent, man-made changes in the local environment. Therefore, it is possible that random differentiation in partly isolated populations has contributed to the local differences in buff–gray ratios. The difference in gene ratio between Alamogordo and Lone Butte mice (Table IV) possibly results from such random divergence. Mutation rates of the genes under study are unknown, so the possible role of differential mutation rates in the present situation cannot be considered.

Differential selection of the two genes is the third possible cause of the observed differences in gene frequencies. One is dealing here with two genes having major effects on the gross appearance of the mice. The buff gene (G) produces a buff mouse. The gray gene (g), in duplex quantity, produces a gray mouse. It is to be expected that a buff mouse would have a better chance of escaping detection by predators on buff or red soil than would a gray mouse on the same soil. A gray mouse would stand a better chance of survival on gray soil than would a buff mouse. It has been demonstrated recently that under experimental conditions certain predators do capture more gray than buff deer-mice on buff soil and more buff than gray mice on gray soil (Dice, 1947). It should prove profitable, therefore, to examine the colors of the soils on which the Tularosa mice were living for a clue to the reasons for the differences in gene ratios.

Most of the desert soils in this part of the Tularosa Basin are some shade of pinkish gray in appearance (Map 1). The darkest of these pinkish gray soils occur at the edge of the basin, as shown in the transect, south of Alamogordo and from about six miles north of Tularosa north beyond the limits of the transect. Toward the interior of the basin these pinkish gray soils become paler and exceed all other soils of the area in paleness except the creamy white gypsum of the White Sands. In sharp contrast to these pale, predominantly gray soils, there is an area of dark, brick red soil just north of the town of Tularosa. This area of dark red soil is about four miles wide and extends out about five miles from the base of the foothills into the basin. At its northern limit the dark red soil changes abruptly to pinkish gray. At its southern limit the dark red changes abruptly to light red soil that extends south for about seven miles and merges gradually into pinkish gray.



Map 1. Localities at which samples of deer-mouse populations were taken in the Tularosa Basin, New Mexico. Black rectangles indicate collecting stations. Measurements of soil colors (reflection meter readings) are given for all localities at which soil samples were taken. Values are given for reflected red, green, and blue, respectively.

The Tularosa sample came from about the middle of the area of dark red soil. The relatively high frequency (56.76 per cent) of buff genes and the low frequency (43.24 per cent) of gray genes I believe to be directly related to selection by predators against the nonadaptive gray gene on the dark red soil. In this population the ratio of buff, adaptive to gray, nonadaptive phenotypes, as estimated from the sample, is 81.5 to 18.5 per cent. Actually, the selection has favored not only an adaptive gene but also an adaptive genotype. The buff Tularosa mice are a darker, more saturated buff than are the buff mice from the gray soils, as has been shown by colorimetric methods. These methods, while they do show differences, fail to show the full difference to the human eye between the Tularosa buff mice and most of those from the gray soils. Most of the Tularosa buffs have a dark, reddish buff pelage in contrast to the less saturated and grayer buff of most buff mice from gray soils.

On the dark red soil near Tularosa, I believe that natural selection has favored buff over gray mice and that it has also favored the accumulation of the minor, additive intensifiers of pigment.

The Alamogordo and Lone Butte populations occupy pinkish gray soils. The comparatively high frequencies of gray genes in these populations (75.13 per cent at Alamogordo, and 63.54 per cent at Lone Butte) I attribute to selection by predators against the nonadaptive buff on the pinkish gray soils. As on the Tularosa red soil, selection is favoring an adaptive genotype rather than a single gene. The buff mice of the gray soils are paler than those of the dark red soils. It is possible that once fixation of the buff–gray genes has occurred in these populations of the gray soils, selection has operated principally against the minor intensifiers. It appears that some of the buff mice of the pinkish gray soils, as affected by the minor, modifying genes, are less conspicuous on these soils than are gray mice on the dark red soil.

The high frequency of gray genes (75.87 per cent) in the White Sands population, as estimated from the small sample, possibly indicates the selective advantage of gray over buff on the White Sands. The buff and gray mice are both relatively conspicuous on the white gypsum, and any selective advantage of gray over buff must be of a lesser magnitude than the advantage of one color type over the other on the other soils of the basin. The buff–gray ratio in the White Sands population is to be expected whether or not there is selection for either color type. The White Sands undoubtedly received its original population of deer-mice from near-by populations of the pinkish gray desert soils, and I suspect that the deer-mouse population on the gypsum dunes occasionally approaches zero only to be replenished from populations such as that at Lone Butte. With gene fixation in these populations and with no selection for or against buff or gray on the White Sands, the gene frequencies on the sands would parallel the frequencies in the near-by populations.

The Salinas sample obviously is not consistent with the other samples from the Tularosa Basin. Here, on pinkish gray soil of approximately the same appearance as the Alamogordo soil, there is a buff–gray ratio and an average shade of pelage no different from the gene ratio and the shade of pelage in the population of the dark red Tularosa soil. One must either weaken the case for natural selection as the principal agency in establishing and maintaining the observed gene frequencies in the Tularosa Basin populations or find a reasonable explanation for the situation in this population. The population dynamics of deer-mice in this part of the basin offer such an explanation.

The Tularosa and Salinas samples were taken only four miles apart. There must be relatively free interchange of genes among the deer-mice living in the grassy washes parallel to the railroad. From fragmentary and minimum records it is known that deer-mice frequently move at least one-third of a mile under conditions of moderate population pressure in the mesquite association (Blair, 1943b), and it is likely that they disperse farther than this. Under the conditions of crowding and high population pressure present in the grassy washes, it seems likely that dispersal is over much longer distances.

If natural selection is operating against the buff gene in the Salinas population, then the pressure of immigration from the Tularosa population must be of such magnitude as to obliterate the effects of selection. The buff–gray ratio in the deer-mouse populations along the railroad north of the town of Tularosa consequently would be controlled by selection on the dark red soil. There is other evidence to support this theory. The deer-mouse population at Tularosa was much larger than at Salinas. Only a little more than one-half as many mice were caught at Salinas as at Tularosa (Table II) even though more effort was expended and more territory was covered there than at the latter station. It has been shown experimentally that, given differential population pressures within an ecological association, immigration will proceed mostly from the areas of greater to the areas of lesser pressure (Blair, 1940). There apparently was such a pressure differential between the Salinas and Tularosa populations at the time the samples were taken, and the dispersal pressure from the Tularosa toward the Salinas population probably was considerably in excess of the reverse pressure. The populations were at a peak of abundance when the samples were taken, but this difference in relative population size and a consequent pressure differential would be maintained even under reduced densities of population. It is almost axiomatic that, as population sizes fluctuate, the relative densities of the species in minor subdivisions of a local area maintain their relative proportions. It is quite possible that, with seasonal decreases in population size in the area, the Salinas population becomes very low only to be later replenished by immigration from the relatively larger Tularosa population. The difference in the size of the two deer-mouse populations appears to be due to minor differences in the grassy wash association at the two stations.

The grass cover is thicker at Salinas than at Tularosa, and this condition seemed to favor another, related species. The wood mouse (*Peromyscus leucopus tornillo*) was enormously abundant at Salinas and much less numerous at Tularosa.

The contrasting situations at Salinas and Alamogordo, respectively four miles north and eighteen miles south of the Tularosa station, emphasize the important role of isolation by distance and of population structure in differentiation. Adaptive and even random nonadaptive differentiation may occur under isolation by distance alone (Wright, 1943). Under conditions of partial isolation and selection within the different populations, differentiation will occur faster than under the action of partial isolation or selection alone (Wright, 1938). This situation in nature is illustrative of these processes. The Salinas and Tularosa populations, which are only four miles apart, are estimated to have the same parameters in respect to buff–gray gene frequencies and in respect to minor, modifying, color genes, even though selection pressure is assumed to be exerted in opposite directions in the two populations. I conclude that immigration pressure exceeds selection pressure and that, as discussed above, immigration pressure probably is unequal between the two populations. The Alamogordo population, eighteen miles away, is no more isolated from the Tularosa mice except by distance than is the Salinas population. Thus, while a distance of four miles is not sufficient for differentiation, even under presumably heavy selection pressures, a distance of eighteen miles is sufficient under the conditions in this area, which include differentiation into several vegetation and soil types. The genetic balance between the populations along this transect, as it exists today, probably is influenced by the linear distribution of a part of the populations. Such a distribution of the species favors differentiation more than does areal distribution (Wright, 1943). The frequencies of buff and gray presumably were fixed in the populations long before the railroad was built and under conditions of greater isolation than exist today. The Tularosa and Alamogordo populations do, however, maintain their distinctness, even though a linear route of ready dispersal now exists between their two areas. In the Alamogordo population, then, I conclude that selection pressure balances immigration pressure, whereas in the Salinas population selection pressure is swamped by the pressure of immigration from the more abundant population of the Tularosa red soil.

In summing up this discussion I conclude that the differences in buff–gray gene ratios and the quantitatively determined differences in minor, modifying genes in the Tularosa Basin populations are attributable to: (1) partial isolation of relatively small local populations in favorable ecological associations that are separated by considerable expanses of unfavorable associations, (2) selection by predators against nonadaptive color genotypes, and (3) the combined effects of isolation by distance and ecological isolation. Populations only four miles apart, on differently colored soils, and not isolated, except by distance and relatively linear distribution, show no differentiation in buff–gray gene ratio. Populations eighteen miles apart, on differently colored soils, isolated only by distance, and having a relatively linear distribution do show adaptive differentiation in the frequency of the buff and gray genes.

SUMMARY

Deer-mice (*Peromyscus maniculatus blandus*) were trapped alive at five stations in the Tularosa Basin, New Mexico, and brought into the laboratory for a study of gene frequencies in wild populations. These mice carry Mendelian alleles, buff (G) and gray (g), that have major effects on pelage color, and which presumably have different survival values on differently colored soils.

Genotypes of the dominant buff mice were determined by test crosses in as many of the buff mice as possible. Not all the mice produced offspring, and the gene frequencies were, therefore, estimated by means of a maximum likelihood formula appropriate to data in which only a part of the dominants are classified as to genotype.

A chi-square test of the data revealed no significant departure from genetic equilibrium in any of the populations. Significant differences in buff–gray ratios were present between each of three populations living on pinkish gray soil and each of two other populations living on or near an area of dark red soil.

The differences in gene ratios are attributed to the effects of: (1) partial ecological isolation of the deer-mice into relatively small, local populations, (2) differential selection for the two genes by predators on red and pinkish gray soils, (3) the combined effects of ecological isolation and isolation by distance. Populations only four miles apart showed no differentiation even though selection was presumably operating in opposite directions in the two populations. Differentiation in buff–gray frequencies and in minor color characters was evident in populations fifteen to eighteen miles apart and living on differently colored soils.

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